



# The functional decoupling of processes in alpine ecosystems under climate change

Loïc Pellissier<sup>1,2</sup> and Sergio Rasmann<sup>3</sup>

Climate change may promote the decoupling of the different above-ground and below-ground compartments of high elevation ecosystems. Along elevation gradients, a trade-off between species tolerance to cold climates and metabolic rates dictates that cold adapted organisms display a lower efficiency in decomposition, growth or herbivory. As a consequence, if dispersal or evolution under climate change is systematically faster for agents of one compartment (e.g. insect herbivores, or soil microbes, respectively) compared to others, novel and more efficient functions will arise in the alpine systems and increase fluxes of elements to and through this compartment. We illustrate this potential decoupling using a mechanistic model, where the efficiency of agents in the compartments follows the metabolic theory. To detect and forecast ecosystem decoupling under climate change, we argue that the current efficiency of agents should be measured systematically along elevation gradients. In addition, future research should investigate the impact of dispersal and evolution in response to climate change on ecosystem processes.

## Addresses

<sup>1</sup> Landscape Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland

<sup>2</sup> Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland

<sup>3</sup> Laboratory of Functional Ecology, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland

Corresponding author: Rasmann, Sergio ([sergio.rasmann@unine.ch](mailto:sergio.rasmann@unine.ch))

Current Opinion in Insect Science 2018, 29:126–132

This review comes from a themed issue on **Global change biology**

Edited by **Oswald J Schmitz** and **Adam E Rosenblatt**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 17th July 2018

<https://doi.org/10.1016/j.cois.2018.07.005>

2214-5745/© 2018 Elsevier Inc. All rights reserved.

## Introduction

Climate change is not only impacting species distributions worldwide [1,[4<sup>•</sup>]], but how species interact within food webs [3]. Ecosystem processes are primarily controlled by energy-mediated metabolic efficiency [4<sup>•</sup>], but they are also limited by the functional composition of species in communities [5<sup>•</sup>]. Climate change could therefore influence ecosystem processes by: first, modifying

temperature and precipitation regimes and subsequent nutrient distribution, second, increasing metabolic efficiency facilitating the fluxes among the different trophic compartments [6,7], or third, modifying the efficiency of the different trophic compartments via the arrival and/or evolution of more efficient novel organisms. Hence, the colonization of previously unsuitable habitats under climate change can form novel biotic interactions [3,8–10,11<sup>•</sup>], and also induce changes in ecosystem processes [12,13<sup>••</sup>]. A number of recent models have incorporated biotic interactions for predicting species distribution and abundance under climate change [14,15]. However, those models do not usually include how species turnover and novel interaction or functions might impact ecosystem processes [16]. In contrast, mechanistic, compartment-based, models can produce expectations on how the shifts in available energy or metabolic efficiency influence the fluxes among compartments, or their size, in ecosystems [17–19]. A limitation of these models, however, is that they do not consider how novel functions — arising through the incursion of new agents into an ecosystem or through *in situ* evolution — could reshape ecosystem processes. Forecasting the effect of climate change on ecosystem processes requires considering the direct temperature effect on the metabolism of organisms with the indirect effect of novel species ecological or evolutionary responses to temperature [3,[4<sup>•</sup>],20].

Novel functions in a given ecosystem may arise from two main processes; first, dispersal into the focal ecosystem allowing the colonization of novel habitats from fast niche-tracking species [21,22<sup>•</sup>], and second, selection and evolution within the focal ecosystem for higher metabolic efficiency [23,24]. Under climate change, more proficient insect herbivores can move into alpine ecosystems, where such trophic interactions are generally weaker [22<sup>•</sup>,25]. Moreover, given strong novel ecological pressures, standing genetic variation and short generation times, some species (e.g. soil microbes) may evolve new functions over ecological time scales potentially impacting ecosystem processes [26]. Here, we propose that a modified functional efficiency arising in an ecosystem via dispersal and/or evolution might desynchronise fluxes among trophic compartments under climate change. In particular, climate change could modify ecosystem-level dynamics through the decoupling of herbivores or soil microorganisms with the plant compartment. Below, we review the co-variation of biotic and abiotic factors along ecological gradients — elevation in mountain systems — for dissecting the direct effect of temperature increase on

decomposition rate, plant productivity, herbivory and elemental cycling from the additional effect of unsynchronised dispersal and evolution among trophic compartments.

### Ecosystem structure along elevation gradients

The properties of the different ecosystem compartments vary sharply when moving from low to high elevation [27], and offer the necessary natural variation for providing expectations on the effect of climate change on ecosystems in the near future [28] (Figure 1). Species assemblages along elevation gradients are characterized by strong beta diversity [29,30], culminating in dramatic species turnover at the treeline [e.g. 30–34]. Paralleling compositional turnover, plant functional diversity also varies along elevation, but patterns are much more idiosyncratic and trait specific [35,36]. Functional turnover within different trophic compartments, such as plants [35], herbivores [30] or microorganisms [37], is also reflected in the relative size (energy/matter) of each compartment. Typically, the abundance of herbivores decreases toward the alpine belt [38]. Therefore, it is expected that the role of herbivores — at least for arthropods — on ecosystem functioning in the alpine environment is less pronounced than in warmer and more stable habitats [39]. Because plant–herbivore interactions are reduced at high elevation, it was postulated that plants should also produce lower levels of defences [33], which results in a general increased plant palatability at high elevation [40,41]. Nonetheless, elevational patterns in plant resistance against insect herbivory vary depending on the type of toxic chemicals produced [25,42].

Soil-related properties and processes also vary along elevation gradients [37,43] (Figure 1). Particularly, across the treeline boundary drastic changes appear, largely mediated by temperature-driven variation in carbon and nitrogen stocks and microbial activity in the soil [27]. Soil depth, nutritive value and microbial diversity all decreases, but carbon, nitrogen and root biomass per volume of soil tend to be higher at high elevation [44,45], indicating slower organic matter decomposition, slower mineralization rate, higher carbon sequestration [28] and lower efficiency of cold-adapted decomposers [46] at higher elevation. To summarize, plant productivity at the species and community level [47], insect herbivory [48], decomposition from soil organisms [49] all decrease with elevation, while organic matter and carbon storage increases. As a consequence, the size of the different compartments [28], but also the speed of the processes [50], largely varies below compared to above the treeline. The overall functioning of the alpine ecosystem is slower than at low elevation [51,52], since it is expected to be largely mediated by physiological trade-offs. As species evolved to tolerate cold and harsh environments, they are constrained to reduce their overall metabolism [38,44,53,54].

### Climate change and the decoupling of plant–soil–herbivore dynamics

As a consequence of climate change, the processes at high elevation may slowly tend toward those of low elevation, but additional ecological and evolutionary effects might accelerate this dynamic by; first, directly increasing metabolic activity under warmer temperatures, or second, indirectly decoupling the efficiency between compartments. More specifically, a rapid dispersal of herbivores toward higher elevation following climate warming could increase herbivory rates resulting in reduced plant biomass [20]. Similarly, soil warming could stimulate decomposition and nutrient cycling if the activity of decomposers is directly under the influence of temperature [55]. Moreover, higher temperatures might select for micro-organisms that are more efficient under the new temperature conditions [26], further increasing decomposition rates. If warming increases soil nutrient availability, it may indirectly enhance plant nutritional status, in turn affecting aboveground plant–insect–enemy interactions, depending on the feeding mode and diet breadth of the insects, as well as on how plant endogenous defenses themselves respond to warming [9].

We illustrate the direct and indirect effect of temperature increase on ecosystem functioning in an alpine system using a mechanistic model involving soil microbe decomposers, plants and herbivores inspired from [56,57]. In addition to previous work focusing on the functioning of the ecosystem [58], we here explore how climate change might influence ecosystem functioning directly, or indirectly via a shift in the parameters of the metabolic

Figure 1

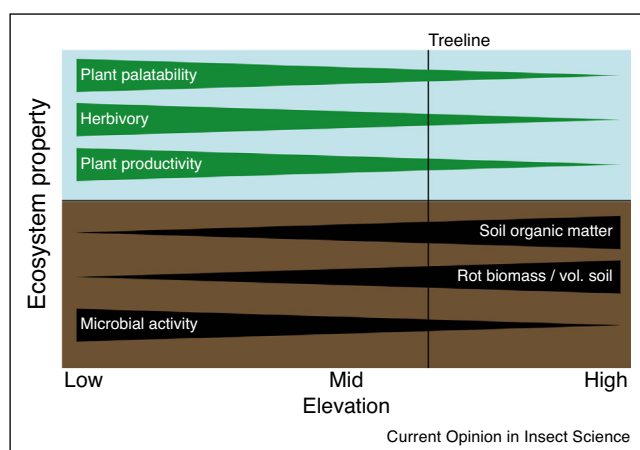


Illustration of compartment variation above and below the treeline. The depicted trends are based on multiple syntheses of ecosystem processes along elevation gradients [e.g. 25,37,39,41,44,75].

function of trophic compartments. We expect two types of responses: (1) a direct effect of climate change on organism metabolic rates considering a stable metabolic function, (2) an indirect effect involving a new metabolic function either following (2.1) the colonization of insect herbivore from lower elevation [25], or (2.2) newly evolved efficiency expected in soil microbes with short generation times and potentially faster evolutionary rate [26]. Assuming generalizable temperature-metabolic rates functions, we expect that climate change might accelerate metabolic rates proportionally across trophic levels. As a consequence, given no species dispersal or evolution and assuming equivalent metabolic rates, the trophic compartments should display proportional increase under climate change, except for the dead organic matter, which should decrease [28]. In contrast, under scenarios of migration or evolution, the metabolic rates of one compartment will change (Figure 2a), potentially causing a shift in the relative proportion of the other connected trophic compartments. We illustrate those

expectations following the model defined by this set of equations:

$$\frac{dM}{dt} = m_P \times P + (1 - \Delta_H) \times f_H(T, T_{min,H}) \times H \times P + m_H \times H - \Delta_D \times f_D(T, T_{min,D}) \times D \times M$$

$$\frac{dD}{dt} = \Delta_D \times f_D(T, T_{min,D}) \times D \times M - m_D \times D$$

$$\frac{dN}{dt} = m_D \times D - f_P(T, T_{min,P}) \times P \times N \quad (1.1)$$

**Figure 2**

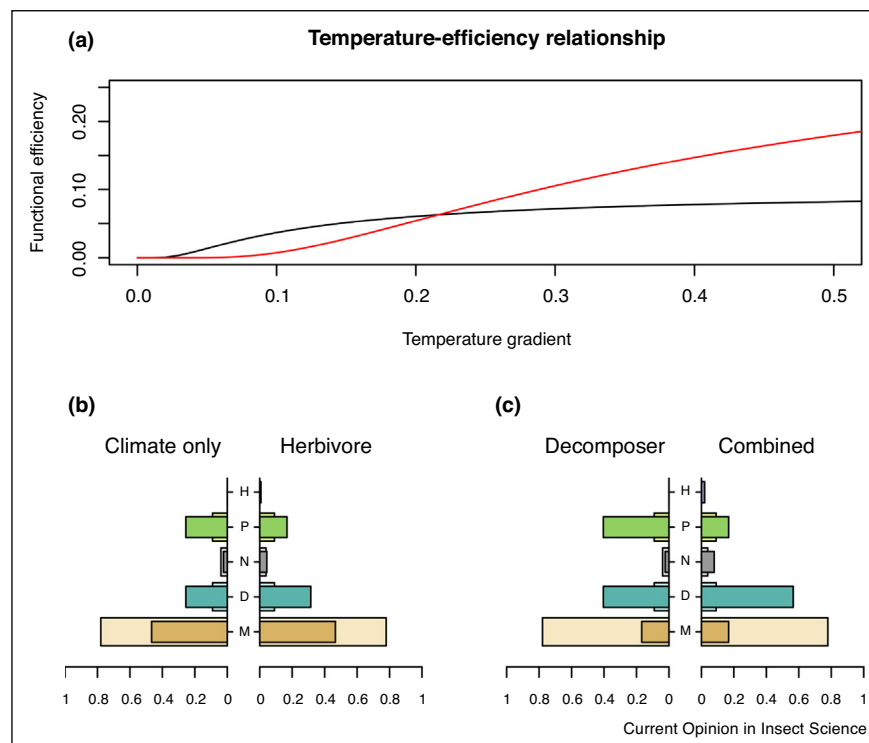


Illustration from a simple ecosystem model (Modified from [58]). Panel (A) shows how functional efficiency  $f$  is negatively related to the minimum temperature  $T_{min}$  that an organism can tolerate with  $T_{min} = 0.1$  in black and  $T_{min} = 0.4$  in red. Panel (B) 'climate only' shows the direct effect on temperature increase on the efficiency and implication for the sizes of the different above-ground and belowground compartments of the ecosystem (H = herbivory, P = plant, N = soil nutrients, D = soil microbes decomposers, and M = dead organic matter). 'Herbivore' indicate the effect of increased metabolic functions from  $T_{min} = 0.1$  to  $T_{min} = 0.6$  of the herbivore compartment. Panel (C) 'soil microbes Decomposer' shows the additional effect of soil microbes decomposer evolution from  $T_{min} = 0.1$  to  $T_{min} = 0.6$  for increased efficiency under climate change, while 'combined' shows the combined effect of soil microbes decomposers and herbivores. Lighter coloured bars indicate baseline data without climate change, while darker coloured bars indicate expected values with climate change. We illustrated the model with a mortality of 0.1, 5% of processed plant into biomass by the herbivore, a value of temperature of 0.1 and an effect of climate change increase of +0.55. These represent illustrative values as we currently lack ecosystem data to calibrate the model.

$$\frac{dP}{dt} = f_P(T, T_{min,P}) \times P \times N - m_P \times P - f_H(T, T_{min,H}) \times H \times P$$

$$\frac{dH}{dt} = \Delta_H \times f_H(T, T_{min,H}) \times H \times P - m_H \times H$$

In this model, the ecosystem is assumed to be limited by a single nutrient  $N$ . The dead organic matter ( $M$ ) is supplied by the plant organic matter ( $P$ ), the plant biomass not eaten by the herbivore ( $H$ ), and the dead herbivore. We assume that only a fraction  $\Delta_D$  of the dead organic matter can be readily processed by the microbes as suggested by studies of soil systems, where decomposers are rarely limited by available material, so that only <5% of the soil organic matter is actually microorganism decomposers [59]. Nutrient is supplied by the mortality of the decomposers. The herbivores  $H$  are feeding on the biomass  $P$  of the plants and only a fraction  $\Delta_H$  of the plant is assimilated into herbivore biomass [60]. This fraction is expected to be around 5–10% [60]. The fraction  $(1 - \Delta_H)$  of non-assimilated plants by the herbivores returns to the dead organic matter compartment.

The resource uptake of detritivores, plants and herbivores depends on their respective stocks and functional responses to resource availability, which is modulated by temperature (Figure 2a). The latter are represented by the type 1 functions  $f_D(T, T_{min,D})$ ,  $f_P(T, T_{min,P})$  and  $f_H(T, T_{min,H})$ . We define the following metabolic function trading-off temperature tolerance and efficiency:

$$f = T_{min} \times e^{-T_{min}/T} \quad (1.2)$$

In which, the metabolic efficiency  $f$  relates to the minimum temperature  $T_{min}$  that an organism can tolerate via a trade-off function (Figure 2a). This function is derived from the metabolic theory where metabolic rates increase exponentially with temperature [61]. In particular, ectothermic insect herbivores may display increased metabolic rate under warmer climates [62], translating into higher feeding rates [63]. Similarly, microbes should display increased metabolic rate under warmer temperature [64]. Compared to Van't Hoff–Arrhenius relation [65], the current formulation is simpler, where the pre-exponential factor and activation energy correspond to  $T_{min}$ . This simplification is necessary since the exact shape of the metabolic response is unknown [66,67]. We can nevertheless assume that species with higher  $T_{min}$  have a generally higher efficiency at warmer temperature, but a slower activation along a temperature gradient. We explored the following scenarios: first, a direct effect of temperature while conserving the current

$T_{min}$ , second, a direct effect of temperature combined with a high functioning of the herbivore compartment through the colonisation of species with higher  $T_{min}$  from lower elevation, and third, the evolution of a higher efficiency, but with a higher  $T_{min}$  in microorganisms because of the trade-off between  $f$  and  $T_{min}$  (Figure 2a).

As an illustration, we modelled the system with a set of parameters producing realistic compartment relative sizes. We used temperature increase from 0.1 to 0.65. The mortality values of decomposers, plants and herbivores were set to 0.1. We further assumed 5% of processed plant into biomass by the herbivore, and only 5% of readily available organic matter to the soil microbes. The increase in herbivore efficiency was determined by a shift from  $T_{min} = 0.1$  to  $T_{min} = 0.6$ , the same for soil microbes. As we are currently lacking all ecosystem data to calibrate such a model, those parameters are illustrative and unitless. Nevertheless, we argue that such exercise can help refine expectations on empirical systems. We evaluated numerically that models from different initial conditions converge to similar equilibria, and report the average of 1000 runs with different initial compartment biomasses (Figure 2b,c).

Within this modelled system, the soil organic matter has the largest compartments (Figure 2b), because the efficiency of microbial detritivores is lower than in warmer conditions [68]. The direct effect of climate change (temperature increase) is expected to increase the efficiency the soil microbe decomposers, increasing the available nutrient for plant growth and adding biomass in both above-ground and belowground compartments (Figure 2b). In contrast, supplying a higher metabolic efficiency of herbivores (i.e. a higher  $T_{min}$  in equation 1.2), which simulates the movement of herbivore from lowland, disproportionally increases the metabolic efficiency of the herbivore compartment, and, in turn causes a higher flux from the herbivore compartment to the soil detritivores, and nutrient compartments (Figure 2b). Corroborating experimental evidence [69], the simulation therefore suggests that an increase in herbivore efficiency (e.g. through herbivore colonization from low elevation) might favour soil resources accumulation, indirectly, through a higher attack rate on plants. The simulated results further agree with the findings of Belovsky and Slade [70], where higher insect herbivory accelerates nutrient cycling and available nutrient [70]. A major consequence of such an effect in alpine system is that the reduction of plant biomass due to herbivory might make it easier for plant colonizers from lowland to invade [22\*]. Furthermore, the increase in decomposed elements in the soil could facilitate the germination and growth of seedlings from lowland invaders. Therefore, we expect that the upward movement of herbivores will cause a decoupling in the fluxes of resources across compartments. Moreover, the evolution of more efficient soil



microbes decomposers (i.e. a higher  $T_{min}$  in equation 1.2) resulted in a strong increase in the flux from the soil organic matter, to nutrients and plants (Figure 2c), and is therefore expected to increase the productivity of the alpine ecosystem [71]. Finally, the combined effect of increased herbivore and soil microbial decomposer efficiency both reduces plant biomass and facilitates the flux of energy from the dead organic matter to the herbivore compartment suggesting a synergetic effect [72].

A major limitation of our illustration is that experimental tests of shift in compartment efficiency under climate change and the consequence on ecosystem functioning was rarely performed [73]. As a consequence, the current model structure and choice of the parameter is arbitrary and experimental quantification of ecosystem functioning is required. Moreover, while we expect the metabolic activity of organisms, including soil meso-fauna and macro-fauna (not included in this model) to shift with increased temperature, it is unclear how their thermal adaption curves might differ from soil microorganisms [2]. Metabolic activity curves should be further quantified across key groups responsible for ecosystem functioning. Similarly, heritability and evolutionary rates should be further quantified to provide an expectation on evolutionary potential [74]. Only such characterization would allow forecasting of the complex responses of ecosystem processes under climate change, accounting for community reshuffling and evolution.

## Conclusions

Climate change is expected to alter biodiversity and ecosystem processes, particularly in environments dominated by stress-tolerant species as those found above the treeline. Herbivores, through their dispersal abilities, and underground organisms, through their faster generation time, might respond ecologically or evolutionarily faster to climate change than other compartments and generate decoupling of current ecosystem processes. It remains unclear whether plants can also show evolutionary adaptations, or plasticity, to seize the new opportunities of faster fluxes of nutrients [10]. Indeed the soil is predicted to be more rich in nutrient and as such, it might also create ecological and evolutionary opportunities for plants to counterbalance increased metabolic activity and higher herbivore attack. Future research along elevation gradients (Box 1) should thus address the combined effect of increased metabolic activity, coupled with novel species interactions in the context of climate change.

## Conflict of interest statement

Nothing declared.

## Acknowledgements

We thank Will Petry for insightful comments. This work was supported by a Swiss National Science Foundation grant [31003A\_159869] to SR, and grant [31003A\_162604] to LP.

### Box 1 Forecasting community composition and ecosystem functioning along environmental gradients during climate change — what remains to be done:

- Coupling dispersal ecology with ecosystem functioning through network ecology.
- Standardize methods for measuring functional traits in plants and higher trophic levels that mediate ecosystem processes.
- Measure efficiency of organisms of different compartments along manipulated temperature gradients.
- Assess rapid evolutionary responses to temperature of different organisms occupying different compartments of the ecosystems.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as

- of special interest
- of outstanding interest

1. Parmesan C, Yohe G: **A globally coherent fingerprint of climate change impacts across natural systems.** *Nature* 2003, **421**:37-42.
2. Parmesan C: **Ecological and evolutionary responses to recent climate change.** *Annu Rev Ecol Evol Syst* 2006, **37**:637-669.
3. Tylianakis JM, Didham RK, Bascompte J, Wardle DA: **Global change and species interactions in terrestrial ecosystems.** *Ecol Lett* 2008, **11**:1351-1363.
4. Glazier DS: **Is metabolic rate a universal 'pacemaker' for biological processes?** *Biol Rev* 2015, **90**:377-407.
- Excellent review on the relationship between biological processes and temperature.
5. Guerrero-Ramírez NR, Eisenhauer N: **Trophic and non-trophic interactions influence the mechanisms underlying biodiversity–ecosystem functioning relationships under different abiotic conditions.** *Oikos* 2017, **126**:1748-1759.
- This works addresses how biotic and abiotic conditions influence the shape of the biodiversity–ecosystem function.
6. Montoya JM, Raffaelli D: **Climate change, biotic interactions and ecosystem services.** *Philos Trans R Soc B Biol Sci* 2010, **365**:2013-2018.
7. van der Putten WH, de Ruiter PC, Martijn Bezemer T, Harvey JA, Wassen M, Wolters V: **Trophic interactions in a changing world.** *Basic Appl Ecol* 2004, **5**:487-494.
8. Schweiger O, Settele J, Kudrna O, Klotz S, Kuhn I: **Climate change can cause spatial mismatch of trophically interacting species.** *Ecology* 2008, **89**:3472-3479.
9. Pincebourde S, van Baaren J, Rasmann S, Rasmont P, Rodet G, Martinet B, Calatayud P-A: **Plant–insect interactions in a changing world.** In *Advances in Botanical Research Series: Insect–Plant Interactions in a Crop Protection Perspective*, vol 81. Edited by Sauvion N, Calatayud P-A, Thiéry D. Elsevier, GBR; 2017:289-332.
10. Rasmann S, Pellissier L: **Adaptive responses of plants to insect herbivores under climate change.** In *Climate Change and Insect Pests. CABI Climate Change Series*, vol 7. Edited by Björkman C, Niemelä P. CABI; 2015:38-53.
11. Thompson PL, Gonzalez A: **Dispersal governs the reorganization of ecological networks under environmental change.** *Nat Ecol Evol* 2017, **1**:0162.
- Strong theoretical framework for how dispersal mediated the distribution of ecological interactions.

12. Petchey OL, McPhearson PT, Casey TM, Morin PJ: **Environmental warming alters food-web structure and ecosystem function.** *Nature* 1999, **402**:69.
  13. Morin X, Fahse L, Jactel H, Scherer-Lorenzen M, García-Valdés R, Bugmann H: **Long-term response of forest productivity to climate change is mostly driven by change in tree species composition.** *Sci Rep* 2018, **8**:5627.
- Excellent modeling approach for disentangling direct and indirect effects of warming on diversity-ecosystem relationship.
14. Brooker RW, Travis JM, Clark EJ, Dytham C: **Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change.** *J Theor Biol* 2007, **245**:59-65.
  15. Pellissier L, Descombes P, Hagen O, Chalmardier L, Glauser G, Kergunteuil A, Defosse E, Rasmann S: **Growth-competition-herbivore resistance trade-offs and the responses of alpine plant communities to climate change.** *Funct Ecol* 2018, **0**.
  16. Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes J-A, Guisan A *et al.*: **The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling.** *Biol Rev* 2013, **88**:15-30.
  17. O'Connor MI, Selig ER, Pinsky ML, Altermatt F: **Toward a conceptual synthesis for climate change responses.** *Glob Ecol Biogeogr* 2012, **21**:693-703.
  18. Yvon-Durocher G, Allen AP: **Linking community size structure and ecosystem functioning using metabolic theory.** *Philos Trans R Soc B: Biol Sci* 2012, **367**:2998-3007.
  19. Wang S, Brose U: **Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis.** *Ecol Lett* 2018, **21**:9-20.
  20. Van der Putten WH, Macel M, Visser ME: **Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels.** *Philos Trans R Soc B Biol Sci* 2010, **365**:2025-2034.
  21. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J *et al.*: **Herbivory in global climate change research: direct effects of rising temperature on insect herbivores.** *Glob Change Biol* 2002, **8**:1-16.
  22. Alexander JM, Chalmardier L, Lenoir J, Burgess TI, Essl F, Haider S, Kueffer C, McDougall K, Milbau A, Nuñez MA *et al.*: **Lags in the response of mountain plant communities to climate change.** *Glob Change Biol* 2018, **24**:563-579.
- Addresses the effect of several 'lag' factors on plant community reshuffling during climate change.
23. Holt RD: **The microevolutionary consequences of climate change.** *Trends Ecol Evol* 1990, **5**:311-315.
  24. Hoffmann AA, Sgro CM: **Climate change and evolutionary adaptation.** *Nature* 2011, **470**:479-485.
  25. Rasmann S, Pellissier L, Defosse E, Jactel H, Kunstler G: **Climate-driven change in plant-insect interactions along elevation gradients.** *Funct Ecol* 2014, **28**:46-54.
  26. Wallenstein MD, Hall EK: **A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning.** *Biogeochemistry* 2012, **109**:35-47.
  27. Mayor JR, Sanders NJ, Classen AT, Bardgett RD, Clément J-C, Fajardo A, Lavorel S, Sundqvist MK, Bahn M, Chisholm C *et al.*: **Elevation alters ecosystem properties across temperate treelines globally.** *Nature* 2017, **542**:91.
  28. Sundqvist MK, Sanders NJ, Wardle DA: **Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change.** *Annu Rev Ecol Syst* 2013, **44**:261-280.
  29. Pellissier L, Ndiribe C, Dubuis A, Pradervand J-N, Salamin N, Guisan A, Rasmann S: **Turnover of plant lineages shapes herbivore phylogenetic beta diversity along ecological gradients.** *Ecol Lett* 2013, **16**:600-608.
  30. Descombes P, Vittoz P, Guisan A, Pellissier L: **Uneven rate of plant turnover along elevation in grasslands.** *Alpine Bot* 2016:1-11.
  31. Guo Q, Kelt DA, Sun Z, Liu H, Hu L, Ren H, Wen J: **Global variation in elevational diversity patterns.** *Sci Rep* 2013, **3**:3007.
  32. McCain CM, Grytnes JA: **Elevational gradients in species richness.** *eLS* 2010.
  33. Pellissier L, Fiedler K, Ndiribe C, Dubuis A, Pradervand J-N, Guisan A, Rasmann S: **Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients.** *Ecol Evol* 2012, **2**:1818-1825.
  34. Girardin CAJ, Farfan-Rios W, Garcia K, Feeley KJ, Jørgensen PM, Murakami AA, Cayola Pérez L, Seidel R, Paniagua N, Fuentes Claros AF *et al.*: **Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects.** *Plant Ecol Divers* 2014, **7**:161-171.
  35. Pellissier L, Fournier B, Guisan A, Vittoz P: **Plant traits co-vary with altitude in grasslands and forests in the European Alps.** *Plant Ecol* 2010, **211**:351-365.
  36. de Bello F, Price JN, Muenkemüller T, Liira J, Zobel M, Thuiller W, Gerhold P, Goetzenberger L, Lavergne S, Leps J *et al.*: **Functional species pool framework to test for biotic effects on community assembly.** *Ecology* 2012, **93**:2263-2273.
  37. Pellissier L, Niculita-Hirzel H, Dubuis A, Pagni M, Guex N, Ndiribe C, Salamin N, Xenarios I, Goudet J, Sanders IR *et al.*: **Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps.** *Mol Ecol* 2014, **23**:4274-4290.
  38. Hodkinson ID: **Terrestrial insects along elevation gradients: species and community responses to altitude.** *Biol Rev* 2005, **80**:489-513.
  39. Rasmann S, Alvarez N, Pellissier L: **The altitudinal niche-breadth hypothesis in insect-plant interactions.** In *Annual Plant Reviews, Insect-Plant Interactions*, vol 47. Edited by Voelckel C, Jander G. John Wiley & Sons, Ltd; 2014:339-359.
  40. Pellissier L, Roger A, Bilal J, Rasmann S: **High elevation *Plantago lanceolata* plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature?** *Ecography* 2014, **37**:950-959.
  41. Descombes P, Marchon J, Pradervand J-N, Bilal J, Guisan A, Rasmann S, Pellissier L: **Community-level plant palatability increases with elevation as insect herbivore abundance declines.** *J Ecol* 2016, **105**:142-151.
- Large-scale multi-species analysis on plant palatability variation along elevation gradients.
42. Pellissier L, Moreira X, Danner H, Serrano M, Salamin N, van Dam NM, Rasmann S: **The simultaneous inducibility of phytochemicals related to plant direct and indirect defences against herbivores is stronger at low elevation.** *J Ecol* 2016, **104**:1116-1125.
  43. Seibert J, Stendahl J, Sørensen R: **Topographical influences on soil properties in boreal forests.** *Geoderma* 2007, **141**:139-148.
  44. Körner C: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems.* Berlin: Springer; 2003.
  45. Malhi Y, Girardin CAJ, Goldsmith GR, Doughty CE, Salinas N, Metcalfe DB, Huaraca Huasco W, Silva-Espejo JE, del Aguilla-Pasquell J, Farfán Amézquita F *et al.*: **The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective.** *New Phytol* 2017, **214**:1019-1032.
- Excellent analysis on the mechanistic causes for the observed productivity decline trend along elevation gradients.
46. Rubenstein MA, Crowther TW, Maynard DS, Schilling JS, Bradford MA: **Decoupling direct and indirect effects of temperature on decomposition.** *Soil Biol Biochem* 2017, **112**:110-116.

47. Malhi Y, Girardin CA, Goldsmith GR, Doughty CE, Salinas N, Metcalfe DB, Huaraca Huasco W, JE Silva-Espejo, Aguilla-Pasquell J, Farfán Amézquita F: **The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective.** *New Phytol* 2017, **214**:1019-1032.
  48. Galmán A, Abdala-Roberts L, Zhang S, Berny-Mier y Teran JC, Rasmann S, Moreira X: **A global analysis of elevational gradients in leaf herbivory and its underlying drivers: effects of plant growth form, leaf habit and climatic correlates.** *J Ecol* 2017. n/a-n/a.
  49. Looby CI, Treseder KK: **Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest.** *Soil Biol Biochem* 2018, **117**:87-96.
  50. Pappas C, Fatichi S, Burlando P: **Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter?** *New Phytol* 2016, **209**:137-151.
  51. Stige LC, Kvile KØ: **Climate warming drives large-scale changes in ecosystem function.** *Proc Natl Acad Sci* 2017, **114**:12100-12102.
- Excellent documentation of how warming could alter ecosystem functioning through species replacement.
52. Grimm NB, Chapin FS, Bierwagen B, Gonzalez P, Groffman PM, Luo Y, Melton F, Nadelhoffer K, Pairis A, Raymond PA et al.: **The impacts of climate change on ecosystem structure and function.** *Front Ecol Environ* 2013, **11**:474-482.
  53. Clarke A: **Temperature and the metabolic theory of ecology.** *Funct Ecol* 2006, **20**:405-412.
  54. Hille SM, Cooper CB: **Elevational trends in life histories: revising the pace-of-life framework.** *Biol Rev* 2015, **90**:204-213.
  55. Del Toro I, Ribbons RR, Ellison AM: **Ant-mediated ecosystem functions on a warmer planet: effects on soil movement, decomposition and nutrient cycling.** *J Anim Ecol* 2015, **84**:1233-1241.
- Direct evaluation of climate warming impact on ecosystem processes, indirectly mediated by an arthropod ecosystem engineer.
56. Loreau M: **Biodiversity and ecosystem functioning: a mechanistic model.** *Proc Natl Acad Sci U S A* 1998, **95**:5632-5636.
  57. de Mazancourt C, Loreau M: **Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: should a palatable plant evolve?** *Evolution* 2000, **54**:81-92.
  58. Loreau M: **Linking biodiversity and ecosystems: towards a unifying ecological theory.** *Philos Trans R Soc Lond B Biol Sci* 2010, **365**:49-60.
  59. Chapin FS III, Matson PA, Mooney HA: **Terrestrial decomposition.** *Principles of Terrestrial Ecosystem Ecology.* New York: Springer; 2002, 151-175.
  60. Schoonhoven LM, van Loon JJA, Dicke M: *Insect-Plant Biology.* Oxford: Oxford University Press; 2005.
  61. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB: **Toward a metabolic theory of ecology.** *Ecology* 2004, **85**:1771-1789.
  62. Dillon ME, Wang G, Huey RB: **Global metabolic impacts of recent climate warming.** *Nature* 2010, **467**:704-U788.
  63. DeLucia EH, Nabity PD, Zavala JA, Berenbaum MR: **Climate change: resetting plant-insect interactions.** *Plant Physiol* 2012, **160**:1677-1685.
  64. Price PB, Sowers T: **Temperature dependence of metabolic rates for microbial growth, maintenance, and survival.** *Proc Natl Acad Sci U S A* 2004, **101**:4631-4636.
  65. Arrhenius SA: **Über die dissociationswärme und den einfluß der temperatur auf den dissociationsgrad der elektrolyte.** *Z Phys Chem* 1889, **4**:96-116.
  66. Irlich UM, Terblanche JS, Blackburn TM, Chown SL: **Insect rate-temperature relationships: environmental variation and the metabolic theory of ecology.** *Am Nat* 2009, **174**:819-835.
  67. Chown SL, Marais E, Terblanche JS, Klok CJ, Lighton JRB, Blackburn TM: **Scaling of insect metabolic rate is inconsistent with the nutrient supply network model.** *Funct Ecol* 2007, **21**:282-290.
  68. Pomeroy LR, Wiebe WJ: **Energetics of microbial food webs.** *Hydrobiologia* 1988, **159**:7-18.
  69. Chapman SK, Hart SC, Cobb NS, Whitham TG, Koch GW: **Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis.** *Ecology* 2003, **84**:2867-2876.
  70. Belovsky G, Slade J: **Insect herbivory accelerates nutrient cycling and increases plant production.** *Proc Natl Acad Sci* 2000, **97**:14412-14417.
  71. Parton W, Schimel DS, Cole C, Ojima D: **Analysis of factors controlling soil organic matter levels in Great Plains Grasslands 1.** *Soil Sci Soc Am J* 1987, **51**:1173-1179.
  72. Wurst S: **Plant-mediated links between detritivores and aboveground herbivores.** *Front Plant Sci* 2013, **4**.
  73. Stevnbak K, Scherber C, Gladbach DJ, Beier C, Mikkelsen TN, Christensen S: **Interactions between above- and belowground organisms modified in climate change experiments.** *Nat Clim Change* 2012, **2**:805.
  74. Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM et al.: **A framework for community and ecosystem genetics: from genes to ecosystems.** *Nat Rev Genet* 2006, **7**:510-523.
  75. Kergunteuil A, Campos-Herrera R, Sánchez-Moreno S, Vittoz P, Rasmann S: **The abundance, diversity and metabolic footprint of soil nematodes is highest in high elevation alpine grasslands.** *Front Ecol Evol* 2016, **4**.